PAN-PACIFIC ENTOMOLOGIST
63(3), 1987, pp. 247–255

The *Drosophila* Fauna of a Native California Forest (Diptera: Drosophilidae)

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INTRODUCTION

During the years since *A.D.* 1492 and especially during the past 150 years the *Drosophila* fauna of North America has undergone considerable change. Two major factors have contributed to this change: (1) a number of *Drosophila* species from other continents have become introduced into the fauna, e.g. *D. melanogaster* and *simulans* and recently *D. subobscura*; and (2) larval substrates have changed both qualitatively and quantitatively. Numerous fruits and vegetables from other continents have been introduced, e.g. European grapes, apples, and citrus, all of which provide substrates for native polyphagous species, e.g. *obscura* species group. In contrast urbanization, agriculture and lumbering have reduced the volume of substrates provided by forest fungi, slime fluxes, cacti and fermenting bark. It is reasonable to assume that the population sizes of most oligophagic and monophagic species have been reduced. The *virilis* species group provides a clear example of such a reduction in population size (Spieth 1979).

Blodgett Forest

The Blodgett Forest Research Station of the University of California Department of Forestry and Conservation is located in the Eldorado National Forest on the western slope of the Sierra Nevada Mountains. Consisting of 2,961 acres (1198 hectares) located between 4,100 and 4,600 feet (1250–1400 m) elevation, it is a "mixed conifer" forest which supports ponderosa pine, sugar pine, white fir, incense cedar, douglas fir, black oak, tan oak and native shrubs and forbs. The forest is totally surrounded by the Eldorado National Forest. The sole access to Blodgett is via a narrow two lane road that originates at Georgetown, a small town located 10 air miles west of Blodgett. Continuous forest exists from Georgetown to Blodgett. A number of dwellings, mostly summer homes plus camping areas, exist along the access road, mainly along the western portion. Agricultural activities are absent along the road and in the surrounding forest.

The Blodgett Station was established in 1933, and since its inception *all* introduced plants have been systematically eliminated. Thus, as a result of the Blodgett Station's location within the National Forest and the efforts of the foresters, it can reasonably be assumed that the forest approaches closely the habitat that existed when Columbus reached America.

Systematic collecting of the *Drosophila* fauna was undertaken during the years 1981–84 in order to determine both the species composition and size of the *Drosophila* fauna of the forest.

Collecting Procedures

Blodgett Forest is an irregularly shaped rectangle with a north-south axis of circa 4.5 mi (7.2 km.). A network of unpaved dirt roads facilitates access to various portions of the forests. Five sites along a north-northwest to south-southeast transect were selected.

Two sites, 1 and 1A, at the northern end of the forest, with elevations of 1310 m and 1320 m, are located 375 m apart. The forest is of medium density with numerous individuals of the native black oak, *Quercus kelloggii,* which are scattered among the conifers.

Site 2, elevation 1365 m, is located 2.6 km southward of sites 1 and 1A. It slopes westward and has a grove of *Q. kelloggii* surrounded by a coniferous forest amongst which are numerous oaks and shrubs.

Site 3, elevation 1292 m, located 840 m south-eastward of site 2, is beside a stream in a dense forest of mature conifers. Oaks are totally absent and daily temperatures are consistently 2–3°C lower than at any other area of the forest.

Site 4, elevation 1310 m, is located 1.31 km. south of site 3. The terrain slopes south-eastward. Soil depths in the western part of the area are shallow with numerous rocky outcrops. Numerous young *Q. kelloggii* oaks and *Ceanothus sp.* dominate this upper, drier and rocky western portion of the area while old mature oaks and a mixture of young oaks and conifers are present in the lower eastern portion.

Plastic, red colored buckets, height 26 cm, dia. 21.5 cm, were used as bait traps, and fermenting, yeasted bananas as bait. Three buckets spaced 100–200 m apart were used at each of the five sites. The bait buckets were suspended from tree branches 0.5–1.5 m above the forest floor. Collections were scheduled to be accomplished at two-week intervals from mid-April to early October during 1981, '82, '83 and '84. Each collection consisted of an "evening" collection followed by a "morning" collection on the following day. The bait buckets and baits were removed at the termination of the "morning" collections. Occasionally one or both collections were nonproductive due to environmental conditions such as low temperatures, high temperatures or the rare passage of a weather front through the area.

All specimens collected at each of the 15 baits were returned to the laboratory for identification. Since the four species of the *D. obscura* species group cannot be effectively separated visually, individuals belonging to the group were identified by electrophoretic techniques.

Blodgett Forest Species

During the four years, 1981–84 inclusive, adults of 13 species belonging to three subgenera, i.e. *Dorsilopha, Drosophila* and *Sophophora,* were collected (Table 1).

Subgenus **Dorsilopha** Sturtevant

A single male specimen of *D. busckii* Sturtevant was collected 6.vi.82 (Table 1). *D. busckii* is a cosmopolitan "garbage" species. This single individual can reasonably be considered to have been a migrant into the Blodgett Forest.

Subgenus **Sophophora** Sturtevant

Adults of two species of the *melanogaster* species group and four species of the *obscura* species group were collected during each of the four years (Table 1).

SUMMARY OF SPECIES

Table 1

Subgenus	Species	1981		1982		1983		1984	
		♂	♀	♂	♀	♂	♀	♂	♀
Dorsilopha	*D. busckii*	0	0	1	0	0	0	0	0
Sophophora									
	D. melanogaster ♂♂	5	–	4	–	5	–	38	–
	D. simulans ♂♂	53	–	6	–	104	–	165	–
	D. melanogaster								
	D. simulans ♀♀		118		32		262		1387
	D. azteca								
	D. miranda	1290	1410	1049	1040	1500	2170	1075	973
	D. persimilis								
	D. pseudoobscura								
Drosophila									
	D. californica	7	7	11	14	378	282	84	47
	D. immigrans	2	35	0	5	9	53	0	3
	D. montana	0	0	0	1	0	1	0	1
	D. occidentalis	143	129	51	34	162	143	167	138
	D. pinicola	249	20	56	67	60	50	38	45
	D. subfunebris	4	13	0	1	3	10	3	14

Melanogaster species group

D. melanogaster Meigen and *D. simulans* Sturtevant

During all four years adults of both species were absent from the collections during the months of April, May, June and July (Table 2). Presumably they were also absent during the winter and early spring. Only two males, one of each species, plus 32 females were collected during August and 30 of these females during August of 1984 (Table 2). In each of the four years the number of females greatly exceeded the number of males collected, i.e., 4.7 females for each male. Also the number of *simulans* males greatly exceeded the number of *melanogaster* males.

Blodgett Forest is located in the drainage of the Sacramento Valley. At the lower elevations vast acreages of the valley are devoted to vineyards, orchards and vegetable crops, especially tomatoes. Each year huge populations of both *D. melanogaster* and *D. simulans* develop in these agricultural areas. The *simulans* populations greatly exceed in size the *melanogaster* populations. Areas located about 15–20 miles southwest and west of Blodgett are known to produce large populations of both of these species. After the fruits and vegetables are harvested the adults must seek other food and ovipositional sites. The appearance of adults of the two species in the Blodgett Forest in September and October during each of the four years suggests that these individuals were migrants from lower elevations and that they must have migrated at least 15–20 miles. Further, the lack of individuals of both

Table 2

Species		Year	Apr	May	June	July	Aug	Sept	Oct	Totals
D. melanogaster	♂♂	1981	0	0	0	0	0	0	5	5
		1982	0	0	0	0	0	4	0	4
		1983	0	0	0	0	0	2	3	5
		1984	0	0	0	0	1	37	0	38
										52
D. simulans	♂♂	1981	0	0	0	0	0	38	15	53
		1982	0	0	0	0	0	6	0	6
		1983	0	0	0	0	0	8	96	104
		1984	0	0	0	0	1	162	2	165
										328
D. melanogaster *D. simulans*	♀♀	1981	0	0	0	0	2	94	22	118
		1982	0	0	0	0	0	32	0	32
		1983	0	0	0	0	0	95	167	262
		1984	0	0	0	0	30	1352	5	1387
										1749

species during the months of April through July indicates that the migrants that reach Blodgett during the months of August through October of the preceding year were not able to survive in the forests during the winter months.

Obscura species group

Four species of the *obscura* group are residents of the Blodgett Forest: i.e. *D. azteca* Sturtevant and Dobzhansky, *D. miranda* Dobzhansky, *D. persimilis* Dobzhansky and Epling and *D. pseudoobscura* Frolowa. Numerically they are the dominant species of the forest (Table 1).

Morphologically, individuals of *D. persimilis* and *D. pseudoobscura* are essentially indistinguishable. Undersized individuals of *D. miranda* can be confused with large sized individuals of *persimilis* and *pseudoobscura.* Only the males of *azteca* can be confidently identified. The electrophoretic patterns of each of the four species, however, are species specific and therefore were utilized to determine the specific identity of the flies (Table 3). *D. pseudoobscura* and *D. persimilis* are numerically the dominant members of the *obscura* species constituting more than 70% of the *obscura* flies collected during 1981, '82 and '83 but receding to 61% in 1984. In comparison *D. miranda* increased from 6.88% in 1981 to 23.26% in 1984. *D. miranda* is a "northern" species whose range extends from Canada to the southern portion of California. In comparison *D. azteca* is a "southern" species whose range extends from Guatemala to northern California. From 1981 to 1983 the *azteca* populations decreased sharply but recovered in 1984 (Table 3).

No specimens of the recently introduced *D. subobscura* were collected during the years 1981–84. During 1985 a few collections were made in the forest and *D. subobscura* appeared in one of these.

Table 3
D. obscura group species

	1981	1982	1983	1984
D. pseudoobscura	36.28%	27.16%	44.35%	30.85%
D. persimilis	34.64%	47.83%	32.66%	30.29%
D. miranda	6.88%	13.74%	20.80%	23.26%
D. azteca	22.20%	11.27%	2.19%	15.60%

Subgenus **Drosophila**

Six species of the subgenus were collected (Table 1). Each of these is a member of a different species group.

D. californica Sturtevant

D. californica, a member of the *repleta* species group, was described by Sturtevant (1923) on the basis of 1 ♂ and 4 ♀♀ collected at Pacific Grove, California. Subsequent collecting has indicated that the species is apparently restricted to California. Its larval substrate is unknown and it is considered to be a "rare" species since it appears infrequently and usually in small numbers in *Drosophila* collections.

The volume of the larval substrate present in any area is positively correlated with the size of adult populations of the species that breeds in the substrate; i.e., with rare exceptions *Drosophila* females are capable of producing and ovipositing large numbers of fertile eggs during their normal life spans. Thus the major factor controlling population size is the availability of suitable larval substrate(s).

During 1981 only 14 individuals (Table 4) were collected, 11 of which were collected during July and August. In 1982 25 individuals were collected, but, in 1983, 660 specimens of *californica* were collected. Clearly the amount of larval substrate suitable for *D. californica* increased dramatically in 1983. In 1984 the population receded and only 131 individuals were collected.

D. immigrans Sturtevant

This cosmopolitan species is similar to *D. melanogaster* and *D. simulans* in that it cannot overwinter in the forest. During the four years 107 specimens, 11 ♂♂ and 96 ♀♀, were collected. Of these 1 ♂ and 3 ♀♀ were collected during the months of April through August while the remaining 103 were captured during September and October.

The yearly variation was great: e.g., only three specimens, all females, were captured in 1984, 62 individuals of which nine were males in 1983, five females and no males in 1982 and 35 females and 2 males in 1981. It can reasonably be concluded that all of these individuals were migrants from lower elevation.

D. montana Patterson and Wheeler

Only three females, one each in 1982, 1983 and 1984, were captured. This species utilizes the fermenting bark of the aspen of its larval substrate. Since aspen is lacking

Table 4
D. californica Sturtevant

	Apr		May		June		July		Aug		Sept		Oct		Totals		
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂♂	♀♀	T
1981	1	0	0	0	1	0	3	3	1	4	0	0	0	0	7	7	14
1982	0	0	0	0	3	3	5	6	1	3	2	2	0	0	11	14	25
1983	0	1	3	1	11	19	54	51	88	77	148	117	74	16	378	282	660
1984	1	0	10	9	3	2	11	7	34	22	24	7	1	0	84	47	131
															480	350	830

Table 5
D. immigrans Sturtevant

	July		Aug		Sept		Oct		Totals		
	♂	♀	♂	♀	♂	♀	♂	♀	♂♂	♀♀	T
1981	0	1	0	0	0	33	2	0	2	34	37*
1982	0	0	0	0	0	5	0	0	0	5	5
1983	1	0	0	1	6	46	2	6	9	53	62
1984	0	0	0	0	0	2	0	1	0	3	3

*one ♀ coll. 4 April 81

from the Blodgett Forest these three specimens appear to be migrants from higher elevations where aspen and *D. montana* are both common.

D. occidentalis Spencer and **D. pinicola** Sturtevant

Both species utilize fungi as larval substrates. The Blodgett Forest has a Mediterranean type climate with only scant and unpredictable precipitation during the summer months. As a result the area becomes increasingly desiccated during the summer and early fall. The fungal populations reach their peak during April and May and steadily decline during the remainder of the year. Fungi do exist during the summer months along stream banks and at the outflows of a few permanent springs.

D. occidentalis populations peak during June and July. Except for 1982 its populations were similar in size during each of the other three years (Table 6). In contrast the *pinicola* populations reach their peak during May. *D. pinicola* females become sterile when subjected to temperatures above 18°C (Spieth and Heed 1975). In the Blodgett Forest the *pinicola* populations were largest during May (Table 7) and declined rapidly during the following months, and this decline may be due to temperature constraints. Further, the *pinicola* populations, for unknown reasons, declined drastically during each of the following years after 1981.

D. subfunebris Stalker and Spencer

During the four years only 48 specimens of *subfunebris* were collected (Table 1) and it appears to be the rarest of the native species in the Blodgett Forest. Since,

Table 6
D. occidentalis Spencer

	Apr		May		June		July		Aug		Sept		Oct		Totals		
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂♂	♀♀	T
1981	19	10	36	16	31	25	44	39	3	8	4	9	10	12	147	119	266
1982	1	0	15	5	22	10	10	12	3	3	0	4	0	0	51	54	105
1983	0	0	8	17	34	28	62	51	9	18	4	23	15	2	132	139	271
1984	0	0	6	47	39	27	39	46	22	17	4	3	3	4	113	138	251

Table 7
D. pinicola Sturtevant

	Apr		May		June		July		Aug		Sept		Oct		Totals		
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂♂	♀♀	T
1981	20	18	205	136	6	21	12	18	0	2	3	3	3	8	249	206	455
1982	22	32	28	14	2	5	2	6	1	2	0	0	0	0	55	59	114
1983	3	10	29	11	8	9	16	3	0	3	0	2	7	2	63	40	103
1984	0	1	15	12	12	6	5	14	1	8	0	4	3	0	36	45	81

however, only 10 of the specimens were males it is possible that adult individuals, especially males, are only marginally attracted to fermenting bananas and that the populations may have been considerably larger than the present data indicate.

Larval Substrates

As the summer progresses the forest becomes increasingly desiccated. Thus the stream beside which collecting site 3 is located has sufficient volume to support trout during the months of April and May but ceases to flow during August and September. The stream bed remains somewhat moist and *D. occidentalis* and *D. pinicola* tend to congregate in the area but other species such as *D. californica, D. subfunebris* and the four *obscura* species, i.e. *azteca, miranda, persimilis* and *pseudoobscura,* do not. These species consistently occupy all parts of the forest and this indicates that their larval substrates and food sources are distributed throughout the forest. Clearly the adults of these species are able to find adult nutrients and larval substrates in a desiccated environment which appears to lack any free liquid. It should be noted that climatic conditions in the forest are such that no dew forms during the summer and fall months and none of the plants exhibits guttation.

Carson (1951), Carson et al. (1956) investigated sixty-four slime fluxes on the California black oak *Quercus kelloggii* at Mather, California, which is located 90 miles southeast of and at approximately the same altitude as Blodgett. Twenty-two of the sixty-four fluxes they examined were utilized by *D. persimilis* and/or *D. pseudoobscura* and four by *D. californica.* Slime fluxes are relatively rare at Blodgett, a fact which was confirmed by J. Powell who visited Blodgett. The Blodgett fluxes were consistently inspected during the four years but neither adults nor larvae of any species were found on or in the fluxes.

Quercus kelloggii produces vast numbers of acorns. The majority of these are parasitized by either the coleopteran *Curculio occidentalis* or the lepidopteran *Melissopus latiferreanus*. The larvae of these two species feed on the cotyledons and embryo of the acorn. Shortly after the acorn is shed from the tree the larvae reach maturity and they then cut a small circular escape hole through the shell of acorn, escape and pupate in the soil. Remaining in the parasitized acorn is a mass of soft frass. Acorns, both parasitized and unparasitized, quickly desiccate. Foresters in rearing oaks find it necessary to pluck the mature acorns from the trees, in order to insure that the oak embryo is viable.

In the laboratory if the parasitized acorns are kept moistened *D. melanogaster, D. immigrans* and *D. pseudoobscura* females readily oviposit into the acorn, via the parasite's exit hole and/or the base of the acorn where the vascular elements of the acorn are located. Normal adult flies eventually emerge from such acorns.

D. pseudoobscura and *persimilis* are widespread in California. At lower elevations (e.g. Davis, elevation 50 ft.), they can be collected throughout the year but the populations are small during the summer and early fall months. Both species reach peak population size during the late winter and spring, i.e., during the time of major precipitation.

Dr. William Marshall provided me with a liter of acorns which he had collected during February and March 1983 at Oakmont, California, elevation 250 ft. From these 20 ♂♂ and 12 ♀♀ *obscura* spp. and 4 ♂♂ and 8 ♀♀ of *D. immigrans* emerged. This suggests that at the lower elevations in California acorns during the late winter and early spring probably serve as ovipositional sites.

Basically, *Drosophila* adults have pigmentary patterns that blend with the background of their feeding-ovipositional substrates, e.g. *D. virilis* group species on fermenting bark, *D. mulleri* group species on fermenting cacti. The melanistic coloration of the *obscura* species suggested that perhaps their ovipositional substrates might be on or in the forest soil. Dobzhansky once remarked that he could regularly sweep individuals from the forest floor under oak trees at Mather. A number of species of subterranean fungi exist in the California forests but the number of fruiting bodies are few in comparison to the fungi (mushrooms) whose fruiting bodies are above the surface of the soil. Rodents avidly feed on such fungi and can detect the presence of the hidden fruiting bodies, but human collectors must find them by digging up areas of the forest floor. Such digging at various sites in the forest, totalling more than 100 sq. meters, produced six fruiting bodies representing two specimens each of three different species. Five of the fungal bodies were bisected to determine that they did not contain larvae when collected. These were then immersed in moist sand in one-liter glass jars and allowed to decay. Adults of either *D. pseudoobscura* or *D. persimilis* were then added to the jars. One species of fungus was totally ignored by the females of both species. *D. pseudoobscura* females readily oviposited into the other two species of fungi and more than 150 adults were reared from the fungi. If the fungal material was completely immersed in the sand the females then oviposited their eggs into the sand overlying the fungal body and the emerging larvae then migrated to the fungal material.

D. persimilis essentially ignored the fungi. No F_1 *persimilis* emerged from any of the fungi although dissection of one fungal mass showed a few larvae to be present but none matured to adulthood.

In sum, fungi, acorns and slime fluxes can serve as larval substrates for species of the *obscura* group, but the size of the populations in the Blodgett Forest and elsewhere indicates that there must be other, as yet undiscovered, endemic larval substrates.

SUMMARY

Adults of thirteen species of *Drosophila* were collected in the Blodgett Forest during the years 1981–84. Eight of these species, i.e. *D. azteca, miranda, persimilis, pseudoobscura, californica, occidentalis, pinicola* and *subfunebris* are residents. Adults of the other five species, i.e. *D. busckii, melanogaster, simulans, immigrans,* and *montana* are migrants into the forest.

Numerically the four species of the obscura group are the dominant species in the forest. Intensive search was made for the larval substrates of these species. A few slime fluxes on *Quercus kelloggii* were found but none was used by the flies. Most of the acorns of *Q. kelloggi* are parasitized by either a coleopteran or a lepidopteran. Such acorns, if they are kept moist after the parasite larva has emerged from the acorn, are readily used by *D. persimilis* and *D. pseudoobscura* as larval substrates. Further, some subterranean fungi also can serve as larval substrates for *D. pseudoobscura* but these fungi were not attractive to *D. persimilis.*

ACKNOWLEDGMENTS

This study was supported in part by grant GM2222-1. Forest Manager Robert C. Heald and Robert Timoni of the Blodgett Forest and Ms. Laurie Barr of the Department of Genetics, provided invaluable assistance and advice.

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